

ANALYSIS OF TWELVE SONORAN DESERT SEED
SPECIES PREFERRED BY THE DESERT
HARVESTER ANT

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ABSTRACT

Twelve species of Sonoran desert seeds are shown to be the preferred food of the desert harvester ant, *Veromessor pergandei* (Mayr), at the Deep Canyon Desert Research Center, Riverside County, California. The nutrient and caloric content of these species are analyzed: stepwise extraction of (1) surface lipid, (2) inner lipid, (3) protein, and (4) carbohydrate was followed by extraction by thin layer chromatography of monoterpenoids in the surface lipid fraction. Caloric content was estimated by nutrient content. Monthly records of nutrient intake per ant colony show that with some exceptions, lipid (excluding surface lipid) is taken in greatest proportion and carbohydrate in the smallest. The amount of surface lipid is highly correlated with the content of inner lipid, protein, and carbohydrate, and with the caloric content of the seeds. The amount of surface lipid, along with the monoterpenoids therein, is suggested as possible chemical cues that could be utilized by ants in the selection of seeds.

Seeds have evolved under selection for certain physical and chemical properties to meet demands of dispersal, longevity, defense against predation, germination, and seedling establishment. Some of the chemical requirements are met by reserves of lipids, carbohydrates, and proteins stored in the cotyledons or endosperm of the seeds to provide energy and a source of carbon skeleton precursors (Levin, 1974). These stored substances make seeds an important food resource for many animals.

One of the main consumers of seeds in the deserts of southern California is the desert harvester ant, *Veromessor pergandei* (Mayr). It has been shown that granivorous ants do not select from the seed pool at random (Tevis, 1958; Box, 1960; Willard and Crowell, 1965; Eddy, 1970; Went et al., 1976; Pulliam and Brand, 1975). Although some authors suggest that selection may be based on size (Davidson, 1977), shape (Pulliam and Brand, 1975), or abundance of seeds during the foraging season (Willard and Crowell, 1965; Went et al., 1972; Whitford and Ettershank, 1975; Whitford et al., 1976), some workers believe that forage preference must be related at least in part to chemical properties of the seeds (Tevis, 1958; Nickle and Neal, 1972; Whitford, 1978). This paper reports an analysis of the nutrient content and possible sources of chemical cues available to ants in the seed species most commonly used as food by *V. pergandei*. No such study has been reported previously.

The term "seeds" is applied here not only to true seeds but also to nutlets, achenes, and caryopses that are the functional units being used by the ants (Harper et al., 1970).

METHODS

Seeds were collected from *V. pergandei* foragers at the Deep Canyon Desert Research Station near Palm Desert, Riverside County, California. Each month, all foragers returning to a colony during a five-minute period of each hour of a complete foraging cycle were collected and separated from the items they carried. A minimum of five colonies was sampled each month. Forage items were identified, counted, and stored in glass vials, dry at room temperature. Mean weight per ten seeds of each species was determined.

The availability of seed resources was measured as the actual number of seeds of each species found in the surface litter during each month of the study. This measurement was chosen over seed production estimates because it is from the surface litter that the ants draw the great majority of seeds they collect; no buried seeds are sought or found, and only rarely are seeds harvested directly from plants (Gordon, 1978). Each month, three replicate 225-cm² samples of surface litter were taken along a transect from each of 11 types of foraging areas most typically used by the ants: burrow openings, rock depressions, soil depressions, under fallen cholla, under the canopy of several plant species, and from random interspaces between shrubs. Each sample was sieved, then hand sorted; all seeds and other food items were identified, examined, counted, and stored dry at room temperature. The numbers of items counted were corrected for differences in total area represented by each type of foraging area sampled. Details of these methods are given in Gordon (1978).

A set of approximately 20 seeds of each of the 12 species most commonly used by *V. pergandei* as food was taken from among samples collected from the foragers. Analysis of the seeds' nutrient content was conducted in a stepwise manner, extracting first lipids, then proteins, and finally carbohydrates from the same set of seeds.

Lipids were measured in two separate steps, because the ants may make different use of lipids from the surface than those from within the seeds. Surface lipids were extracted from preweighed seeds in chloroform:methanol (2:1 v/v) for 2-3 minutes. The solvent was evaporated, and the lipid weighed (Harborne, 1973). When the quantity of lipid was too small to be weighed, the extract was redissolved, spotted on filter paper, dried, and spotted with osmic acid to obtain an approximate reading by comparison with spots of known concentration. For some species the capsule, calyx, achene, or floret was also spot-tested with osmic acid and Sudan IV for presence of surface lipids. A similar method was used to extract lipids from inside the

seeds, differing only in that the seeds were first macerated and allowed to stand for six hours before each of three extractions.

Proteins were measured with the Folin-phenol reagent (Lowry et al., 1951; Vasu, 1965). Only soluble proteins were measured; structural proteins, such as in the pericarp or testa, are discarded by ants and were not measured. Samples were read in a spectrophotometer at $\lambda = 660$ nm, and values were calculated from a standard curve.

Carbohydrates were determined by colorimetric methods using phenol in the presence of concentrated sulfuric acid (Dubois et al., 1956). Samples were read in a spectrophotometer at $\lambda = 490$ nm, and values were calculated from a standard curve of known concentrations.

Terpenoids were separated from previously-extracted surface lipids using thin layer chromatography on silica gel adsorbant with a benzene:chloroform (1:1 v/v) solvent, followed by a detection spray of vanillin/H₂SO₄ (Attaway et al., 1965; Stahl, 1969; Harborne, 1973).

An estimate of caloric content was made based on the nutrient constituents rather than by calorimetric methods in an attempt to include only seed parts actually consumed (Spector, 1952; Levin, 1974).

Spearman rank-correlation tests were applied to nutrient and caloric content values of all species.

Mucilage exudation on wetting was tested by placing intact seeds in water with India ink.

RESULTS

Monthly seed use by foragers, compared with a monthly frequency distribution of seed availability in the litter, is summarized in Table 1. A detailed account of the ants' diet and of food availability, including 100 seed species as well as insects and other nonseed material, is given in Gordon (1978).

Seed weight, content of protein, carbohydrate, internal lipid, surface lipid, and calories of the 12 species are shown in Table 2. Protein content in all but three species is below 12 percent by weight. High protein species are *Cryptantha angustifolia* (20.1 percent), *Hyptis emoryi* (16.8 percent), and *Ambrosia dumosa* (12.8 percent). The content of carbohydrate is relatively low for all species, with the highest amount present in the grass *Schismus barbatus* (9.3 percent), followed by *Oenothera claviformis* (6.5 percent). The other species have less than four percent carbohydrate. The internal lipid content is greater than 19 percent in all but three species; the low species are *Plantago insularis* (5.5 percent), *Larrea tridentata* (10.9 percent), and *Schismus barbatus* (4.8 percent). The two lowest of these have no measurable surface lipid; however, qualitative spot tests on the capsule, carpel, and floret of the three indicate a small amount of lipid on the external structures, which are typically encountered by foraging ants prior to or concurrently with the seeds contained therein.

TABLE 1. MONTHLY SEED USE OF 100 SPECIES BY THE DESERT HARVESTER ANT AT DEEP CANYON, RIVERSIDE CO., CA. First number is percent of total seeds foraged, by species (N = 6144); second number is percent of total seeds in litter samples, by species (N = 36,305). Species are designated by initials: *Larrea tridentata*; *Euphorbia micromera*; *Plantago insularis*; *Cryptantha angustifolia*; *Hyptis emoryi*; *Oenothera claviformis*; *Ambrosia dimosa*; *Bebbia juncea*; *Encelia farinosa*; *Perityle emoryi*; *Psathyrotes ramosissima*; *Schismus barbatus*; All Other Species. "p" = less than 1 percent. "*" = no data for month immediately following.

Species	1975												1976			
	JUN	JUL*	SEP	OCT	NOV	DEC*	MAR	APR*	JUN*	AUG	SEP*	NOV	DEC			
<i>L. t.</i>	2, 4	5, 12	31, 16	17, 37	9, 14	43, p	1, p	1, 22	1, 1	1, 12	11, 34	1, 12	0, 8			
<i>E. m.</i>	0, 5	0, 11	0, p	2, 1	0, 2	10, 1	10, 6	0, p	0, p	1, 12	0, 2	0, 17	48, 30			
<i>P. i.</i>	1, 2	17, 1	13, 1	3, 1	17, p	10, p	28, 4	71, 2	1, 1	1, p	25, p	10, 1	14, 1			
<i>C. a.</i>	32, 7	0, 1	2, 5	1, 1	26, 2	0, 2	16, 10	8, p	2, 19	64, 1	0, 6	10, 3	0, p			
<i>H. e.</i>	4, 53	3, 21	8, 5	42, 8	2, 20	1, 5	12, 36	0, 18	11, 39	3, 3	14, 13	0, 39	0, 11			
<i>O. c.</i>	0, p	11, p	14, 1	0, 0	0, p	2, p	0, p	1, p	0, p	2, 1	15, p	0, 0	0, 0			
<i>A. d.</i>	0, 2	0, 2	1, 1	0, 2	0, 6	0, 1	5, 2	0, 4	7, 8	2, 4	13, 4	0, 3	0, 1			
<i>B. j.</i>	11, 6	1, 6	3, 8	3, 5	8, 1	5, 4	2, 11	1, 1	14, 7	1, 6	3, 4	58, 13	4, 40			
<i>E. f.</i>	27, p	22, 5	0, 1	3, 14	0, 2	0, 7	0, 4	0, 23	53, 12	10, 25	5, 23	1, 8	28, 2			
<i>P. e.</i>	1, 2	17, 1	1, 6	0, 2	0, p	0, p	4, 4	0, 4	1, p	0, p	1, 3	2, p	0, p			
<i>P. r.</i>	1, 3	0, p	3, 1	2, p	23, p	15, p	7, 1	0, p	0, p	2, 1	5, 1	14, 1	0, p			
<i>S. b.</i>	7, 9	5, 30	6, 51	9, 26	1, 51	6, 49	5, 3	1, 24	5, 12	5, 20	0, 2	3, 1	5, p			
A.O.S.	7, 7	5, 10	6, 4	9, 3	1, 2	6, 31	5, 19	1, 2	5, 1	5, 15	0, 8	3, 2	5, 7			

TABLE 2. WEIGHT OF TEN SEEDS (W/10); PERCENT COMPOSITION BY WEIGHT OF PROTEIN (P), CARBOHYDRATE (CHO), INTERNAL LIPID (L), AND SURFACE LIPID (SL); CALORIES PER TEN SEEDS (CAL/10); AND CALORIES PER GRAM (CAL/gm) OF 12 SPECIES OF SONORAN DESERT SEEDS. Standard deviation in parentheses. \bar{x} = 3224 (1583) Cal/gm.

Plant species	W/10 (mg)	P	CHO	L	SL	Cal/10	Cal/gm
<i>Larrea tridentata</i>	31.27 (.87)	3.5	2.1	10.9	9.5	62 (1.0)	2013 (56)
<i>Euphorbia micromera</i>	1.35 (.04)	3.5	1.1	36.8	14.7	6 (0.1)	4628 (138)
<i>Plantago insularis</i>	9.88 (.40)	6.5	3.5	5.5	0.0	9 (0.3)	982 (39)
<i>Cryptantha angustifolia</i>	0.65 (.02)	20.1	1.2	29.2	8.9	2 (0.1)	4421 (132)
<i>Hyptis emoryi</i>	2.97 (.13)	16.8	1.0	28.8	29.3	17 (0.7)	5921 (266)
<i>Oenothera claviformis</i>	0.77 (.05)	7.4	6.5	23.1	0.6	1 (0.1)	2323 (81)
<i>Ambrosia dumosa</i>	21.96 (.55)	12.8	1.1	36.8	26.5	120 (3.0)	5494 (37)
<i>Bebbia juncea</i>	8.74 (.26)	8.5	1.5	29.9	24.5	45 (1.4)	5172 (155)
<i>Encelia farinosa</i>	7.56 (.38)	7.3	2.6	23.5	8.4	24 (1.2)	3233 (161)
<i>Perityle emoryi</i>	1.43 (.07)	7.0	1.9	20.9	14.1	5 (0.3)	3440 (172)
<i>Psathyrotes ramosissima</i>	7.14 (.29)	4.3	3.5	19.9	0.0+	15 (0.6)	2083 (83)
<i>Schismus barbatus</i>	0.67 (.03)	4.3	9.3	4.8	0.0	1 (0.0)	1037 (42)

Species with higher lipid content generally show higher surface lipid amounts. In *Hyptis emoryi*, for example, surface lipid constitutes nearly one-third of total seed weight. Not only is the amount of surface lipid highly correlated with that of inner lipid ($r = 0.96$, $p < 0.01$), but also with the amount of protein ($r = 0.92$, $p < 0.01$), carbohydrate ($r = -0.74$, $p < 0.01$), and caloric content ($r = 0.99$, $p < 0.01$) of the seeds.

There are other strong correlations among the nutrient constituents. Protein and internal lipid content of the 12 species are positively correlated ($r = 0.92$, $p < 0.01$); protein and internal lipid contents are each negatively correlated with carbohydrate content ($r = -0.75$, $p < 0.01$; $r = -0.70$, $p < 0.05$, respectively). Jones and Earle (1966) showed that, on a family basis, there is a strong positive correlation between average oil and protein content in seeds. Their data indicate that families low in seed oils and proteins are more likely to include species with starchy seeds than are families rich in oils and proteins. Their generalizations are supported by the data reported here.

Earle and Jones (1962), Kleiman et al. (1964), and Jones and Earle (1966) reported values within 3 percent of those shown in Table 2 for the families represented in the present study, and some are as close as 0.04 percent.

Caloric content of the seeds is expressed for units of ten seeds, and for a gram of seeds for each species (Table 2). There is a wide range of values among the 12 species (982–5921; \bar{x} = 3224, s.d. = 1593). Reichman (1976) reports a higher mean for 18 species of Sonoran desert seeds (\bar{x} = 4579, s.d. = 736), measured by microbomb calorimetry. His direct measure should yield higher values, because structural ma-

TABLE 3. MONTHLY NUTRIENT INTAKE (90-99 PERCENT) AND CALORIC INTAKE (100 PERCENT) PER COLONY PER DAY. Percent nutrient intake is based on total mg of edible material.

Month	Nutrient intake (mg)			Nutrient intake (%)			Caloric intake
	Protein	Lipid	CHO	Protein	Lipid	CHO	Calories
Jun 75	312.5	732.3	857.9	16	39	45	13,804
Jul 75	396.5	848.8	143.4	29	61	10	10,051
Sep 75	270.7	680.2	136.0	24	63	13	12,686
Oct 75	106.5	251.4	37.3	27	64	9	5,425
Nov 75	162.0	402.7	102.2	24	60	16	6,799
Dec 75	115.6	352.6	71.0	21	65	14	6,830
Mar 76	53.9	96.7	54.5	27	47	26	2,614
Apr 76	136.1	126.0	78.3	40	37	23	2,500
Jun 76	388.4	1164.0	92.9	23	71	6	18,067
Aug 76	582.9	983.8	339.6	30	52	18	22,196
Sep 76	257.0	633.5	75.5	27	65	8	10,062
Nov 76	167.5	532.3	51.2	22	71	7	8,618
Dec 76	169.9	519.9	68.7	22	69	9	7,306

terials are burned along with the soluble nutrients. Although Reichman concludes that caloric as well as chemical and nutritional content of the seeds vary independently of seed weight, in the present sample the caloric content is highly correlated with seed weight ($r = 0.83$, $p < 0.01$) as well as internal lipid content ($r = 0.98$, $p < 0.01$).

The 12 preferred species represent 90-99 percent of seeds gathered each month by *V. pergandei* (Table 1). Based on the nutritional content of these species, I calculated the partial monthly nutrient intake per colony per day (Table 3). In addition, I calculated the total calories taken in per colony per day using the determined caloric values of the 12 preferred species and an average caloric value for the remaining 1-10 percent of other seed species gathered each month (Table 3).

Data on terpenoids extracted from seed and fruit surfaces are summarized in Table 4. Although the identity of the compounds could not be determined from these data alone, it is clear that there are five distinct substances present among the species tested. The thin layer chromatography R_f values are given in the table; characterization of the spots with detection spray at 1 min and 30 min is as follows: spot 1, tan to green; spot 2, tan to brown; spot 3, blue to violet; spot 4, blue to violet; spot 5, only at 30 minutes, colored mauve. Only spot 1 showed in UV light. All compounds appear to be monoterpenoids, which are characteristically colorless, water-insoluble, steam-distillable liquids with fragrant odor (Robinson, 1975).

Mucilaginous species include only *Plantago insularis* and *Euphorbia micromera*.

TABLE 4. R_F VALUES OF FIVE TERPENOID SUBSTANCES OF SEEDS AND FRUITS OF 12 SONORAN DESERT SPECIES. Compounds were extracted in petroleum ether and separated by thin layer chromatography using benzene:chloroform (1:1 v/v) solvent.

Plant species	Plant part	$R_f \times 100$				
		1	2	3	4	5
<i>Larrea tridentata</i>	carpel	—	12	—	72	—
<i>Euphorbia micromera</i>	capsule	—	12	—	—	—
	seed	—	12	26	—	streak
<i>Plantago insularis</i>	capsule	0	12	—	77	streak
<i>Cryptantha angustifolia</i>	calyx	—	12	26	72	streak
	nutlet	—	12	27	—	streak
<i>Hyptis emoryi</i>	fruit	0	13	—	77	streak
	nutlet	0	12	26	—	streak
<i>Oenothera claviformis</i>	capsule	0	12	—	77	streak
	seed	—	12	—	—	—
<i>Ambrosia dumosa</i>	achene	—	—	—	—	—
<i>Bebbia juncea</i>	achene	0	12	—	—	streak
<i>Encelia farinosa</i>	achene	—	—	—	—	—
<i>Perityle emoryi</i>	achene	—	12	—	—	—
<i>Psathyrotes ramosissima</i>	achene	0	12	—	72	—
<i>Schismus barbatus</i>	floret	—	12	—	—	—

DISCUSSION

Of the 100 species available in the litter at Deep Canyon, only 50 are ever collected by *V. pergandei* (Gordon, 1978), and of these, only the 12 species discussed here are used with regularity. In certain months, one or a few of these 12 species dominate. For example, in April, 1976, *Plantago insularis* made up 71 percent of all seeds collected; it is a species low in lipid, high in carbohydrate. In August, 1976, 64 percent of all seeds taken were *Cryptantha angustifolia*, the species highest in protein content.

The frequency of occurrence of seeds in the surface litter reflects the frequency with which they are encountered by the foraging ants. Chi-square tests show that there is a highly significant difference between the number of seeds collected in each month ("observed") and the frequency of seeds encountered in the litter ("expected"), regardless of whether the data are pooled by season, by year, or by month (Gordon, 1978, tables 5-5, 5-6). The ants are clearly selective of the seeds they gather, and thus the 12 species used most frequently can be termed "preferred".

Although detailed nutrient requirements of ants are not known, in general the workers take a large share of carbohydrates as an energy source, growing larvae as well as workers take lipids as a source of energy and reserve, while egg-laying queens and growing larvae make most use of proteins for production of new tissue (Abbott, 1978). Thus the seeds, or portions thereof, may be partitioned among members of

an ant colony, depending on their particular needs. Further, nutrient requirements may change with season, depending on the type of activity in which members are engaged, and upon the composition of the colony in terms of age and caste. Monthly or seasonal changes in nutrient use, therefore, are more interesting than the annual total, since these variations should relate to cycles within the colony.

The array of preferred seed species offers the ants a source of all three fundamental nutrients. In most months, lipid is taken in the greatest proportion, and carbohydrate in the smallest (Table 3). Exceptions were in June, 1975, when carbohydrate accounted for 45 percent of nutrient intake and lipid only 39 percent; and in April, 1976, when only 37 percent lipid was taken in along with 40 percent protein and 23 percent carbohydrate. In March, 1976, although lipid was in the highest proportion (47 percent), the amount of carbohydrate taken in was slightly higher than that of protein (27 and 26 percent, respectively). Although these figures might suggest a relation of nutrient intake to worker activity, such as intense worker activity during early summer requiring high carbohydrate intake, or of reproductive effort in April requiring a higher protein intake, there is a major obstacle to such interpretation: the dynamics of seed storage are unknown. Neither the quantity of seeds stored in a nest at any one time, nor the proportion of seeds used immediately is known. Only small numbers of seeds have been recovered from nest excavations (Tevis, 1958; Wheeler and Rissing, 1975) due to the difficulty of exploring *V. pergandei* nests, which exceed 3.5 m depth and 15 m breadth in sandy desert soils (Tevis, 1958). In addition to the factors of colony needs and partitioning of nutrients among castes, the storability of different seed species, with regards to physical and chemical properties of the seeds, probably influences patterns of seed storage and use. Until these patterns are quantified, the basis of seed selection, the seasonal use of nutrients, and food utilization cannot be fully understood in relation to the activity and reproductive cycles of ant colonies.

It is clear, however, that granivorous ants do select particular seed species from among the available seed pool. If their selection is based upon chemical cues, it is important to determine their nature, and to address the question of whether such cues could provide the ants any information about the nutrient contents of the seeds. *V. pergandei* foragers have been shown experimentally to select seeds by chemical cues alone, without benefit of visual or tactile cues (Gordon, 1978). Ants can perceive at least some components of lipids *via* chemical receptors, because certain fatty acids are among the chemicals used as communication signals or as "releasers". For example, necrophoric behavior is released by the "death scent" of deceased ants, which in *Solenopsis saevissima* consists of a mixture including oleic, linoleic, myristoleic, and palmetoleic acids (Wilson et al., 1958). Further, monoterpenoids are among the compounds used by ants for defense and for

attraction of nestmates (Cavill and Robertson, 1965; Gabba and Pavan, 1970). Thus, the surface lipids measurable on the seeds and fruits under consideration, as well as the five monoterpenoid substances present on seed surfaces, are candidates as chemical cues that could be utilized by ants in the selection of seeds.

Essential oils may provide cues for recognition of particular seed species, learned by experience (Tevis, 1958). Indication of nutrient content, however, could rest on detection of the amount of surface lipid present: the amount of surface lipid is highly correlated with the amount of internal lipid, protein, and carbohydrate available in the seed. The ants may, however, simply be attracted to some lipid and/or terpenoid component. Based on what is known of their feeding methods, ants are not likely to utilize surface lipids as a food source (Went et al., 1972). This question warrants further study, both by experimentation and by examination of discarded seed coats for the presence of surface lipids after seed extraction by the ants.

In the coevolution of plants and the animals with which they interact, some secondary plant substances have come to serve as repellents of pest species, while others are attractants to animals acting as dispersal agents (Fraenkel, 1959; Janzen, 1969; Whittaker and Feeny, 1971). Ants are known to be a major nonpassive dispersal agent for the seeds of many species that have elaiosomes (Berg, 1969, 1975; Handel, 1976). Harvester ants collect seeds for food and carry them up to 100 m from the parent plants (Gordon, 1978). Seeds are frequently dropped by foragers and not recovered; partially eaten but still viable seeds, along with intact seeds that were collected but subsequently rejected, are deposited on the refuse pile outside the nest; and seeds may be abandoned in shallow chambers (Went et al., 1972; Wheeler and Wheeler, 1973). By all these methods, *V. pergandei* and other harvester ants inadvertently disperse seeds of some desert plants. This may provide an advantage to the seed species attractive to them, even though many seeds are eaten. Whether or not the surface lipids serve some other function for the seeds, such as acting as an anti-wetting agent, for example, to prevent premature germination in desert soils, there may be selection for their presence simply for chemical communication with potential dispersal agents—the ants.

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LITERATURE CITED

- ABBOTT, A. 1978. Nutrient dynamics of ants. *In*: Production ecology of ants and termites, M. V. Brian, ed., pp. 233-244. Cambridge Univ. Press, New York.
- ATTAWAY, J. A., L. J. BARABAS, and R. W. WOLFORD. 1965. Analysis of terpenes using thin layer chromatography. *Anal. Chem.* 37:1289-1290.
- BERG, R. Y. 1969. Adaptation and evolution in *Dicentra* (Fumariaceae) with special reference to seed, fruit, and dispersal mechanism. *Nytt Mag. Bot.* 16:49-75.
- . 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Austral. J. Bot.* 23:475-508.
- BEROZA, M. 1970. Chemicals controlling insect behavior. Academic Press, New York.
- BOX, T. S. 1960. Notes on the harvester ant, *Pogonomyrmex barbatus* var. *molefaciens*, in south Texas. *Ecology* 41:381-382.
- CAVILL, G. W. K. and P. L. ROBERTSON. 1965. Ant venoms, attractants and repellents. *Science* 149:1337-1345.
- DAVIDSON, D. W. 1976. Species diversity and community organization in desert seed-eating ants. Ph.D. Dissertation, Univ. Utah, Salt Lake City.
- DUBOIS, M., R. A. GILLIES, J. K. HAMILTON, P. A. REBEN, and R. SMITH. 1956. Colorimetric method for determination of sugars and related substances. *Anal. Chem.* 28:350-356.
- EARLE, R. R. and Q. JONES. 1962. Analysis of seed samples from 113 plant families. *Econ. Bot.* 16:221-231.
- EDDY, T. A. 1970. Foraging behavior of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae) in Kansas. Ph.D. Dissertation, Kansas State Univ., Manhattan.
- FRAENKEL, G. S. 1959. Raison d'être of secondary plant substances. *Science* 129:1466-1470.
- GABBA, A. and M. PAVAN. 1970. Advances in chemoreception 1:185. Appleton-Century-Crofts, New York.
- GORDON, S. A. 1978. Food and foraging ecology of the desert harvester ant, *Vermessor pergandei* (Mayr). Ph.D. Dissertation, Univ. California, Berkeley.
- HANDEL, S. 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae) a new North American myrmecochore. *Amer. J. Bot.* 63:1071-1079.
- HARBORNE, J. B. 1973. Phytochemical methods. Chapman and Hall, London.
- HARPER, J. L., P. H. LOVELL, and K. G. MOORE. 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.* 1:327-356.
- JANZEN, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23:1-27.
- JONES, Q. and F. R. EARLE. 1966. Chemical analysis of seeds. II. Oils and protein content of 759 species. *Econ. Bot.* 20:127-155.
- KLEIMAN, R. F., R. EARLE, I. A. WOLFF, and Q. JONES. 1964. Search for new industrial oils. XI. Oils of Boraginaceae. *J. Amer. Oil Chem. Soc.* 41:459-460.
- LEVIN, D. A. 1974. The oil content of seeds: an ecological perspective. *Amer. Naturalist* 108:193-206.
- LOWRY, O., N. M. ROSEBROUGH, A. L. FARR, and R. J. RANDALL. 1951. Protein measurement with the Folin-phenol reagent. *J. Biol. Chem.* 193:265-275.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- NICKLE, D. A. and T. M. NEAL. 1972. Observations on the foraging behavior of the southern harvester ant, *Pogonomyrmex badius*. *Florida Entomol.* 55:65-66.
- PULLIAM, H. R. and M. R. BRAND. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. *Ecology* 56:1158-1166.
- REICHMAN, O. J. 1976. Relationships between dimensions, weights, volumes, and calories of some Sonoran desert seeds. *Southw. Naturalist* 20:573-586.
- ROBINSON, T. 1975. The organic constituents of higher plants, ed. 3. Cordus Press, N. Amherst, MA.

- SPECTOR, W. S. 1956. Handbook of biological data. Saunders, New York.
- STAHL, E. 1969. Thin layer chromatography. George, Allen and Unwin, London.
- TEVIS, L., JR. 1958. Interrelations between the harvester ant, *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39:695-704.
- VASU, B. S. 1965. Variations in the body fluid nitrogenous constituents of *Pisaster ochraceus* (Echinodermata) and *Cryptochiton stelleri* (Mollusca) in relation to nutrition and reproduction. Ph.D. Dissertation, Stanford Univ., Stanford, CA.
- WENT, F. W., J. WHEELER, and G. C. WHEELER. 1972. Feeding and digestion in some ants (*Veromessor* and *Manica*). Bioscience 22:82-88.
- WHEELER, G. C. and J. WHEELER. 1973. Ants of Deep Canyon. Philip L. Boyd Deep Canyon Desert Research Center, Univ. California, Riverside.
- WHEELER, J. and S. RISSING. 1975. Natural history of *Veromessor pergandei*. I. The nest. Pan Pacific Entomol. 51:205-216.
- WHITFORD, W. G. 1978. Foraging by seed-harvesting ants. In: Production ecology of ants and termites, M. V. Brian, ed., pp. 107-110. Cambridge Univ. Press, New York.
- and G. ETTERS HANK. 1975. Factors affecting foraging activity in Chihuahuan desert harvester ants. Environ. Entomol. 4:689-696.
- , P. JOHNSON, and J. RAMIREZ. 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *P. rugosus* (Emery). Insectes Sociaux 23:117-132.
- WHITTAKER, R. A. and P. P. FEENY. 1971. Allelochemicals: chemical interaction between species. Science 171:757-776.
- WILLARD, J. R. and H. H. CROWELL. 1965. Biological activities of the harvester ant, *Pogonomyrmex owyheei*, in central Oregon. J. Econ. Entomol. 58:484-489.
- WILSON, E. O., N. I. DURLACH, and L. M. ROTH. 1958. Chemical releasers of necrophoric behavior in ants. Psyche 65:108-114.

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BOOKS RECEIVED AND LITERATURE OF INTEREST

Hortulus Aliquando: a sometime journal on historical and current horticultural and allied subjects. Published by GRANT DAHLSTROM at Castle Press, 516 N. Fair Oaks Ave., Pasadena, CA 91103. Three numbers have been published to date. Titles include "Plants in the works of Albrecht Dürer (1471-1528)" by W. A. Emboden; "William Roxburgh's plants of the coast of Coromandel" by Ray Desmond; and "Richard Spruce still lives" by Richard E. Schultes.

A Guide to Botanical Resources of Southern California. By JANICE R. BARTEL and SAGE CULPEPPER BELT. Castle Press, Pasadena. Developed by docents and volunteers of the Natural History Museum of Los Angeles County, 900 E. Exposition Blvd., Los Angeles, CA 90009 and available from the museum for \$4.74 postpaid. Reviewed (*Hortulus Aliquando* 2:2. 1977) by W. A. Emboden.